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CONCURRENT OXIDATION AND REDUCTION BY ROOTS¹

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EHRLICH (1), whose results have been verified by others, has shown that oxidation and reduction processes may exist side by side in the animal organism. According to him the functioning protoplasm can oxidize or reduce by means of its oxygen saturated or unsaturated compounds, respectively. Since the difference in metabolism between plants and animals is one of degree only, it is to be expected that the plant cell likewise should exhibit both oxidizing and reducing powers, as has been found to be the case (2). Oxidation has been more extensively studied on account of its more readily recognized significance in life functions. Reduction, however, is probably just as important as oxidation in the economy of the living cell, and is probably just as good an index of life activity. It is most likely that in the living cell oxidation and reduction alternate in quick succession, as DRECHSEL (3-5) has shown to be the case in certain oxidations outside the living body. It is probable that in this continual oxidation and reduction protoplasm suffers no change in its essential properties and thus preserves its identity.

The literature dealing with the oxidizing power of plant juices is voluminous. Within recent years our knowledge of processes going on within the plant has been greatly enlarged by the studies which have been made on the oxidizing enzymes. This work has been comprehensively summarized by CZAPEK (6), BACH (7), KASTLE (8), and CLARK (38).

The study of the oxidizing power of the plant roots in solution cultures, on the other hand, has received less attention. MOLISCH (9) appears to have been the first to demonstrate the oxidizing power of intact roots. He found that the root secretion was

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capable of oxidizing various organic substances such as guaiacol, pyrogallol, and gallic acid. His work showed that there was considerable active secretion on the surface of growing roots and that this secretion had definite powers to effect changes in organic substances. CZAPEK (10) repeated some of the investigations made by MOLISCH and raised some doubt as to the correctness of MOLISCH's conclusions. The fact that roots have oxidizing powers, as set forth by MOLISCH, has been well corroborated, however, by the investigations of RACIBORSKI (11), who used a number of reagents and widely different plants. He did not find a phanerogam, the roots of which did not have the property of extracellular oxidation. Great differences, however, existed between the oxidative powers of different plants.

Two classes of substances have been found useful in showing the oxidizing power of roots in solution culture. The first class comprises certain soluble chromogens which yield upon oxidation insoluble compounds mainly deposited upon the surface of the roots. The second class of chromogens consists of certain substances which give soluble coloring matter as the result of the oxidizing action of the roots, shown by the change from a colorless to a colored compound or by a change from one color to another which is distinctly different. Compounds belonging to the first class are alpha-naphthylamine, benzdine, vanillin, vanillic acid, and esculin. The second class of chromogens is in many respects more useful for oxidation studies, because the intensity of the color and hence the amount of oxidation can be quantitatively expressed. Among these substances are phenolphthalein, aloin, and leucorosolic acid.

When organic substances like alpha-naphthylamine and benzdine in solution of 10 p.p.m. and 5 p.p.m., respectively, are used, the colors due to oxidation are shown on the root. The most marked oxidation is shown by a narrow but very distinct band of color just back of the root cap. Then comes a practically colorless zone and then a broad colored zone, the color becoming less intense toward the upper part of the root. When a 0.04 per cent solution of aloin is used, a diffusion zone of color is at first formed close to the root, but in the course of a few hours the solution, as a

whole, becomes a cherry red, which varies in depth according to the amount of oxidation.

Reduction by roots has been studied but little. Reduction by the tissues of animals and by micro-organisms, on the other hand, has been extensively studied (2). The reagents used to indicate the reducing power of tissue are chromogens, which on reduction by abstraction of oxygen or by the addition of hydrogen yield a leuco-base, such as alizarin blue, indophenol blue, lacmus, methylene blue, indigo carmine, rosanilin, gentian violet; nitrates which are reduced to nitrites; sodium selenite and tellurite, which are reduced to metallic selenium and tellurium; sulphur, which is converted to hydrogen sulphide.

To show reduction we have tried various reagents and have found sodium selenite to be the best medium at our command. The selenite used was sodium selenite Merck and commercial sodium selenite Merck, the latter for the most part. Solutions of 0.25 per cent were first used. The solution reacted alkaline to litmus and phenolphthalein and was toxic to the seedling. When neutralized with hydrochloric acid, however, the toxicity of the selenite was greatly lessened. When seedlings were grown in the sodium selenite solution made neutral to phenolphthalein and of a strength of 0.125 to 0.25 per cent, the parenchyma cells of the ends of the root next to the cap were colored pink in a few hours by the deposit of selenium. The points of emergence of the secondary roots were often colored in the case of the older seedlings. After a lapse of several hours the whole root became somewhat pinkish. In solution of sodium selenite made $n/500$ acid by hydrochloric acid, the deposit of selenium at the tip of the root was very marked. In alkaline solution the reduction was very little. In short, reduction is more marked in slightly acid solutions. Oxidation, on the other hand, is stronger in slightly alkaline solutions.

As judged by the quickness with which the deposit of selenium is made on the root and the extent and intensity of the deposit, the reducing power increases from the time of germination to the sixth or eighth day and then decreases. It is still present in seedlings thirteen days old, the oldest seedling examined. The oxidative power of the wheat seedling, on the other hand, as judged by the

oxidation of aloin, is less in the young seedling and increases with age.

The relative oxidation was determined by placing the seedlings in culture bottles, 10 seedlings to a bottle, with the roots in the aloin solution made by dissolving 400 milligrams in one liter of pure distilled water. In 20 hours the depth of color produced by the red oxidation product was measured in the colorimeter. Taking the reading for the 12-day seedling as 100, the relative oxidation of the 8-day seedling was 81; of the 5-day seedling 48.

Oxidation of aloin by roots is greater in darkness than in light, the relation being in three separate tests with 4, 6, and 9-day seedlings, 100 in the darkness to 75, 70, and 71, respectively.

Nitrates and phosphates increase the oxidizing power of the wheat roots, while potassium salts, especially potassium iodide, decrease it.

TABLE I
EFFECT OF SALTS ON OXIDATION OF ALOIN BY ROOTS

			Relative oxidation
Control in pure distilled water.			100
Sodium nitrate.	50 p.p.m.	NH ₃	135
Potassium sulphate.	50 p.p.m.	K ₂ O	42
Acid calcium phosphate.	50 p.p.m.	P ₂ O ₅	117
Sodium nitrate.	50 p.p.m.	NH ₃ , K ₂ O, P ₂ O ₅	100
Potassium sulphate.			
Acid calcium phosphate.			
Potassium chloride.	50 p.p.m.	KCl	38
Potassium iodide.	50 p.p.m.	KI	20
Iodine.	50 p.p.m.	I	16

In the experiment given in table I, the seedlings were started germinating January 4, and were put into the nutrient solutions January 10. On January 14 the aloin was placed in the solution, and on January 15 the oxidation readings were made.

The accelerating effect on oxidation of a sodium nitrate solution containing the equivalent of 50 p.p.m. of NH₃ and the retarding effect of potassium salts equivalent to 50 p.p.m. K₂O is shown likewise in the case of plants grown in darkness. In this case the plants 6 days old were put into the salt solutions containing 0.04 per cent of aloin, and the experiment continued for 24 hours, when

the depth of the red oxidation product was measured in the colorimeter with the oxidation products of plants growing in carbon-treated water plus aloin as a control.

TABLE II

RELATIVE OXIDATION OF ALOIN BY ROOTS IN DARKNESS AND IN LIGHT

	In darkness	In light
Control.	100	70
Sodium nitrate.	150	105
Potassium sulphate.	70	47
Potassium chloride.	91	60
Potassium iodide.	66	37

Since BIELECKI (12) has shown that nitrates of potassium, ammonium, and calcium added to a solution of peroxidase lead to its passing through a dialyzer in amounts proportionate to the amount of salt added, it may be that the nitrates increase the oxidizing activity of the wheat roots by allowing more of the oxidizing substance to pass into the medium. With alcoholic guaiac as an indicator, we have found a strong peroxidase reaction in the water in which the seedling roots had grown for 24 hours, and a stronger reaction in sodium nitrate solution in which plants have grown the same length of time. This peroxidase reaction does not occur if the culture water is boiled.

The observable action of salts on the reducing action is variable on account of lack of precision of method, though, as a rule, sodium nitrate equivalent to 50 p.p.m. NH_3 gives the quickest and heaviest deposit at the root tip, while potassium salts give the heaviest deposit on the rest of the root. The potassium salts which retard oxidation have little effect on reduction. Thus a potassium iodide solution containing 14.5 p.p.m. K_2O practically inhibited the oxidation of aloin by the roots of 5-day old wheat seedlings, while allowing good reduction of sodium selenite. It would seem, then, that reduction and oxidation may be independent of each other.

Attempts were made to show simultaneous oxidation and reduction by placing the seedlings with the roots in mixtures of sodium selenite and aloin, benzidine, and alpha-naphthylamine, respectively. In mixtures of sodium selenite and alpha-naphthylamine,

the two deposits of color on the roots were so nearly alike that it was difficult to tell whether selenium had been deposited or not in connection with oxynaphthylamine. In solution of benzidine, 5 p.p.m., the roots as a whole had a blue-black appearance, and a heavy ring appeared just back of the root cap. In the same strength of benzidine plus 0.25 per cent sodium selenite, $n/1000$ acid to phenolphthalein, the black oxidation ring at the root tip still appeared, but the roots, as a whole, were pink from the deposited selenium. In 0.04 per cent aloin and 0.15 per cent sodium selenite made $n/500$ acid, some oxidation of the aloin solution occurred and a good reduction of selenite. In aloin and sodium selenite $n/1000$ acid, there was strong oxidation and slight reduction.

The experiments show that it is possible to have oxidation and reduction by the same roots in the same solution. A slightly acid reaction is favorable to reduction, a slightly alkaline reaction favorable to oxidation. Between these acid and alkali limits both processes are demonstrable as occurring side by side.

It has long been supposed that oxidation by the plant roots and plant extracts is due to the presence of oxidizing enzymes, such as the oxidase, peroxidase, and the related catalase. A good review of the literature on cellular oxidation with consideration of the relationship between the enzymes may be found in works of BACH (7) and KASTLE (8).

According to BACH, the oxidase is a mixture of peroxidase and a peroxide-forming substance. The enzymes taking part in cellular oxidation are according to him oxygenase, peroxidase, and catalase. He explains their relationship as follows: (1) In order to have at its disposition a continued source of active oxygen, the living cell produces oxygenases or bodies capable of fixing atmospheric oxygen with the intermediary formation of peroxides; (2) the peroxides thus formed are activated by the peroxidase in the way that hydrogen peroxide is activated by ferrous sulphate; the system peroxidase-peroxide effects the oxidation of substances serving as aliments to the cell, substances which are oxidized with difficulty; (3) in cases which are particularly favorable to the formation of peroxide, excess of which might be injurious to the

cell, the cell generates a third ferment, catalase, which decomposes the peroxide with the liberation of molecular oxygen.

According to MOORE and WHITLEY (13), there is little evidence of the existence of BACH's oxygenase. These workers believe that all juices showing oxidizing properties possess one type of ferment which, since it acts only in the presence of either naturally occurring or artificial peroxide, may be styled a peroxidase. According to them there is no proof of the existence of any other type of enzyme engaged in oxidation processes.

In regard to cellular oxidation, it must be said that nothing absolutely certain is known regarding the composition or nature of the oxidizing substances in plants and the chemistry of the oxidizing bodies is uncertain. Apart from their destruction by heat and by poisons, little is known concerning their enzymotic nature. They do not seem to act as oxygen carriers in the sense of being able to transfer large amounts of oxygen from the air to the oxidizable substance, since the amount of oxidation is increased only slightly by an increase in the amount of oxygen present. Thus the relative oxidation by the roots of plants growing 4 hours in an atmosphere of pure oxygen and of air, respectively, was 100 and 80. The relative oxidation by plants in air and in a partial vacuum of a pressure of 23 mm. of mercury for 4 hours was 100 and 66; growing 19 hours in a partial vacuum, 100 and 74, respectively. In the partial vacuum the plant must oxidize the aloin by means of its intramolecular oxygen. In an atmosphere of carbon dioxide, oxidation was begun early, but this then stopped, and in 16 hours was a mere trace compared to the oxidation by plants growing in aloin solutions in air. Oxygen is necessary for plant oxidation, but a great increase in the amount of oxygen does not greatly increase the oxidation by plants.

Many, if not all, of the oxidations produced by the so-called enzymes can be brought about by non-enzymotic bodies, both organic and inorganic, as first shown by SCHÖNBEIN (14). Organic bodies like benzaldehyde, benzoyl peroxide, succinyl peroxide, pyrogallol acid, and quinone behave like an oxidase, as do peroxides and other salts of inorganic bases such as iron, lead, manganese, etc.

SPITZER (15) attributes the oxidizing power of animal tissue to the nucleoproteid they contain, the oxidizing power of the nucleoproteid being due to the combined iron they contain. In the absence of sufficient oxygen the same nucleoproteid acts as a reducing agent. BERTRAND (16, 17) showed that the oxidizing power of laccase from *Rhus vernicifera* is associated with the presence of manganese, and that laccase of alfalfa, which is poor in manganese, is inactive toward hydroquinone (18). The mixture of a trace of manganese salt and alfalfa laccase had strong oxygen-carrying power where either constituent alone had very little. Other metals such as iron, aluminum, cerium, zinc, copper, calcium, magnesium, and potassium did not increase the oxidizing power of laccase. BERTRAND showed that manganese salts which are easily hydrolyzable are most efficient oxygen carriers. He considered the active oxidase as special combinations of manganese and an acid radical, the latter probably of a proteid nature and partaking of the properties of a ferment. The manganese would be the really active element of the oxidase, while the acid radical would give the ferment the other properties such as solubility and sensitiveness to heat.

According to REY-PAILHADE (19), the reducing ferment which he found in plants, and which he has described under the name "philothion," possesses the properties of the acid albuminoid radical of the oxidases.

In connection with BERTRAND's conception of the action of manganese and our study of the oxidation action of wheat roots, it is interesting to note that manganese has been found by MAUMENÉ (20) in many plants, among them wheat, as a salt of an organic acid. PICHARD (21) and GÖSSL (22) found manganese widespread in plants and animals. On the other hand, VADAM (23) found no manganese in the oxidase of hellebore, but did find iron; SARTHOU (24) found only calcium, iron, and sodium in the oxidase of *Schinus molle*; while DE STOECKLIN (25) could not find manganese in the ash of the oxidase from horseradish. BACH (26) believes he has obtained from molds an active oxidase which is entirely free from iron or manganese. VAN DER HAAR (27), however, doubts the validity of BACH's conclusion as regards the absence of manganese. EULER and BOLIN (28) found that laccase from

alfalfa previously studied by BERTRAND consisted of the neutral salts, mainly calcium, of certain polybasic organic acids, among which glycollic, mesoxalic, citric, malic, and probably glyoxylic acids have been determined.

Numerous inorganic compounds will change tincture of guaiac blue. Among these SCHÖNBEIN (29) mentions the oxides of the noble metals, the so-called superoxides, saltpeter, chromic acid, permanganic acid, etc., lead peroxide, bromine, chlorine, etc. ALSBERG (30) has shown that many salts have the power to change guaiac to a blue oxidation product either directly or with the addition of hydrogen peroxide. MARTINAND (31) finds that oxides of alkalies and alkaline earths which can form peroxides and percarbonates fix oxygen of the air in an active form, and form bodies which give reactions like organic oxidases. Salts of the oxides of metals possessing several degrees of oxidation give the oxidase reaction in their maximum oxidation. The oxidation was retarded by certain salts and especially by traces of sulphuric acid. WOLFF (32) found that colloidal ferrocyanide of iron exerted in certain oxidations a catalytic effect similar to that of natural peroxidases. According to WOLFF and DE STOECKLIN (33), ferrocyanides and sulphocyanates of iron can produce oxidations which can be effected by natural peroxidases, each producing specific oxidations not characteristic of the other. DE STOECKLIN (34) later found that tannate of iron in the presence of hydrogen peroxide can bring about oxidation of such compounds as generally resist the action of any natural peroxidases now known. Among the substances were phenols, cresol, thymol, anisol, carvacrol, guaicol, pyrogallol, eugenol, isoeugenol, and tyrosine.

In work with aloin, we found that a solution of ferric chloride containing 3 p.p.m. Fe gave good oxidation of aloin. Ferrous chloride, even in solutions containing 25 p.p.m. Fe, did not oxidize aloin without the addition of hydrogen peroxide. With the addition of hydrogen peroxide, 1 p.p.m. Fe as FeSO_4 strongly oxidized the aloin. Other salts which have a direct oxidizing action on aloin are manganese dioxide, calcium oxide and carbonate, and magnesium oxide. Aluminum sulphate and chloride in 5 p.p.m. solution oxidized the aloin with the addition of hydrogen per-

oxide. Sodium and potassium hydrate oxidized the aloin slowly. Copper sulphate plus sodium chloride oxidized aloin solutions immediately. On the organic side, benzaldehyde, quinone, piperidine, atropine, etc., oxidize aloin solutions readily.

From what has been said, it can be seen that there is a strong similarity between the oxidizing action of wheat roots and catalyzers like inorganic salts and benzaldehyde and quinone. Probably the similarity is one of analogy only, the methods of oxidations being but different modes of oxygen transference to easily oxidizable bodies.

KASTLE and LOEVENHART (35) concluded that the so-called oxidizing ferment of the potato is not a true enzyme, but is an organic peroxide. They believe that the oxidation phenomena occurring in plants, and probably also in animals, can be satisfactorily explained upon the supposition that the readily autoxidizable substances which they contain are oxidized to the peroxide condition by molecular oxygen, and that the peroxides thus formed in turn give up part of their oxygen to other less oxidizable substances present in the cell. In other words, the process of rendering oxygen active by the living cell is probably brought about in essentially the same way that this is accomplished by phosphorus, benzaldehyde, and other oxygen carriers.

In regard to reduction by the living cell likewise, uncertainty exists as to whether it is brought about by a true enzyme or by non-enzymotic bodies. HEFFTER (36) has given this question much attention and has come to the conclusion that the reducing activities of organisms are not due to enzymes. As in the case of oxidation, reduction processes comparable to those of the living root may be brought about by purely chemical means, as we have previously shown (2).

As regards oxidation and reduction, it may be said that oxidative bodies may be extracted from the plant roots by suitable means. No body which would reduce sodium selenite in the cold could be extracted, however, although the water extracts of the seedlings reduce the selenite on heating. Thus it seems that the reduction of the selenite by the wheat roots is due to the metabolic

activities of the roots *per se*, and is probably due to the presence of some unsaturated compounds comparable to unsaturated fatty acids, dextrose, etc., which are readily oxidized in contact with air, or to substances like organic hydroxyacids and their salts which possess a slight reducing action.

In regard to the significance of the oxidation and reduction in roots, we may say that whatever increases the development of the plant increases oxidation by the roots, and contrariwise, whatever decreases oxidation by the roots decreases the growth of the plant. In short, oxidation is closely connected with the metabolic activities of the roots. It has been shown (37) that in extracts from productive soils oxidation by roots was strong, and in extracts of certain poor soils the oxidation was little, so that from a soil-fertility standpoint oxidation by roots has considerable interest. Oxidation is due undoubtedly to bodies capable of fixing atmospheric oxygen in an active form, perhaps as peroxides, which secondarily oxidize bodies by the transfer of active oxygen to them. Reduction seems to be connected with the inner metabolism of the plant, and is probably brought about by non-enzymotic compounds analogous to the organic hydroxyacids and their salts, which have a reducing action easily demonstrable by their changing of ferric iron to ferrous iron, or to compounds unsaturated in respect to oxygen, which by their avidity for oxygen reduce the oxygen-containing compounds they come in contact with. Oxidation processes are weak in the young seedling, but increase in strength as the seedling grows. Reduction processes, on the other hand, are predominant in the early stages of the seedling's growth, but are less manifest as the seedling develops and oxidation becomes predominant. In certain stages the two processes occur together and can be made manifest either independently or concurrently. Reduction seems to be mostly intracellular. Oxidation, on the other hand, is manifested strongly extracellularly, and seems to be by far the more prominent property of the plant root.

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